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The University of Washington—Center for Quantitative Sciences
The University of Costa Rica—Centro de Investigación en Ciencias del Mar y Limnología
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Working Paper No. 35

"Abundance/Density Equations for
Age-Structured Multicohort
Populations: MCON
(Multiple Cohort N-dimensional model)"
by
Jerald S. Ault and William W. Fox, Jr.
University of Miami

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Fisheries Stock Assessment CRSP

**Abundance/Density Equations for Age-Structured Multicohort Populations
MCON (Multiple COhort N-dimensional model)**

by

Jerald S. Ault and William W. Fox, Jr.

**Division of Biology and Living Resources
Rosenstiel School of Marine and Atmospheric Science
University of Miami
4600 Rickenbacker Causeway
Miami, Florida 33149
USA**

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Introduction

Traditional yield models have gained recognition as generally reliable for describing population demographic processes over a spectrum of temperate sea fish life history classes. The models have embedded within them assumptions regarding constant parameterization and low to nonexistent population interaction. However, population pressures may be more important determinants of fish stock abundance in tropical multispecies environments. Several investigators have demonstrated that intra-specific density-dependence may be a prevalent feature of natural populations (Hassel, 1974; Murdoch et al., 1975; Fox, 1975; Guckenheimer et al., 1977; Botsford & Wickham, 1979; Pope, 1979a,b; Daan, 1975, 1980). There is insufficient quantitative knowledge about functional relationships such as the manner in which demographic characteristics of a given species change with population density (Beverton and Holt, 1957; Paulik, 1972; Pielou, 1977; Keyfitz, 1977). The dynamical behavior of most natural populations is likely to be influenced by their interactions with various age strata of the same species or with interactions with other species. Typically we are uncertain whether we are dealing with a genuinely "single species" situations (May, 1981). Very simple single-species models with minimal data requirements have been touted for providing policy support to fishery institution management in tropical regions (Munro, 1982; Pauly, 1982; 1983), despite the fact that virtually no exploited fish population is ever in a steady state. Traditional management models may not be suitable for tropical environments and most likely fail because the species under consideration are embedded in complex communities. Simultaneous harvesting of large numbers of species in multispecies systems may often manifest complex "catastrophic" system behavior whereby the system is discontinuously transformed to multiple equilibrium states as the harvest rates increase or environmental circumstances alter (Schaffer, 1985). The suspected high levels of species interactions and dependencies among multicohort populations suggests that these populations may not have asymptotic, stable-point equilibria, and as such may vitiate the simple traditional concepts.

Despite the significant numerical modifications of traditional theory gone through in Ault (1988) and Ault & Fox (1988b) to develop a simulation model that seemingly embodied the overt characteristics of tropical fish stocks, the examinations of Ault (op. cit.) and Ault & Fox (1988c) subsequently pointed out that both dynamic pool and logistic assessment classes of autonomous density-independent models may be inadequate or even inappropriate for expressing the dynamics of tropical fishery stocks and thus for formulating management policy. Inadequacy derives from the neglect or condensation of age-structured effects notwithstanding evidence to the contrary which suggested the apparent intrinsic interactions and feedbacks that structured populations actually exhibit. The expected yield from a given single-species fishery cannot be entirely dissociated from the impact of the same stock on the abundance of its predators or food resources (Caddy & Sharp, 1986). Inappropriateness derives from the existence of multiple age groups and multiple spawnings that are life history adaptations reflecting the difficulty of ensuring species survival in *unstable physical* or *hostile biological* environments. For example the Beverton and Holt (1957) model was developed consistent with their days' general dogma regarding autonomous exploited populations. In the model competition was not mathematically treated and was assumed to occur between a species feeding exclusively on a common supply having no dampening effect between cohorts. Concepts like yield per recruit may also be of dubious validity when recruitment is continuous, periodic and may not be time invariant. Traditional fishery yield models treat two of the three main population facets, viz., the production components, separate from a function specific to the stock recruitment relationship (SRR). The appropriate form of a recruitment function, if any, is still subject to considerable debate, particularly in the tropical environment (see Murphy, 1982). With the exception of computer simulation models (e.g. Walters, 1969; Fox, 1973; Huang & Walters, 1983; Hightower & Grossman, 1987; Ault & Fox, in press), rarely are the production and recruitment models merged analytically. The lack of merger preeminates from the point of view that it may be inappropriate to combine a

relatively reliable model with one subject to doubt (Sissenwine & Shepherd, 1987). In the development of a model for a continuously-breeding population differences in the time scales of events acting on the population should be reconciled. Gross misinterpretations of the abundance and productivity of the stock in question may occur when cohort production is on a time scale that is a miniscule portion of the year. Populations may show little or no tendency to converge to the expected equilibrium state(s).

Population dynamics are thought to be a highly redundant, self-sustaining set of processes (Rothschild, 1986). Although the system is complex, with certain structure and parameterization, perturbations appear to result in a return of the system back to the former stable state or region. Populations may be governed by stability inducing and stability governing elements. Governing effects can be viewed in terms of certain solutions for the motion of deterministic systems, called *attractors* (Thompson & Stewart, 1986). An attractor is something which draws in initial conditions from a region surrounding it, called the attractor's *basin of attraction*. Stability denotes the degree to which a system remains in this basin. Stability induction may be associated with the various cohort age strata. Stability governing mechanisms may be functions of the surrounding physical and biological environments, propagating certain potential interactions among the various life stages of a cohort's passage through time. There is a tendency among many population dynamicists and even the 'muddy boots' ecologists to interpret apparently erratic data as either stochastic "noise" or random experimental error. Another alternative is that some simple deterministic models can give rise to apparently chaotic dynamics (May & Oster, 1976; Thompson & Stewart, 1986; May, 1987) (see Figure 1).

Populations are dependent upon the demographic processes at age-specific levels coupled with density-dependent effects such as the availability of resources, competition and predation effects. The probability that interspecific and intraspecific competition may influence the productivity of fish stocks has been widely recognized, the difficulty has been in determining how to assess it. There are a paucity of theoretical or research models on

which to base expectations of population productivity, measured in whatever units, where intraspecific and/or interspecific competition are involved. Mathematical models of competition have been based in large part on the Lotka-Volterra equations describing a system of interacting species. These equations have historical application to fishery biology. The equations utilize mass-action interaction whose magnitude is proportional to the products of the densities of the two interacting species and an associated competition coefficient given a measure of its intensity (Levine, 1976). The Lotka-Volterra principle -- stating that two closely similar species will not both indefinitely be able to occupy essentially the same ecological niche, but that the slightly more "successful" of the two will completely supplant the other eventually -- has had a prominent place in ecological and evolutionary theory (c.f. Kerner, 1961). Yet the mathematical formulation of the principle has been practically limited to the original rudimentary discussion of Volterra (1928, 1938), Lotka (1925, 1932); in the fisheries literature by Larkin (1963) and May et al. (1979); and developed for control theory by Haimovici (1979a). In these, but two species -- of population sizes N_1, N_2 -- are considered to compete according to an extended Verhulst-Pearl scheme:

$$\frac{1}{N_i} \dot{N}_i = \rho_i - \mu_i (a N_1 + b N_2) \quad (1)$$

ordinarily leading to the extinction of one species and dominance of the other at some static population level. Kerner (1961) and Haimovici (1979b) extended the concepts to include three species systems. The most serious deficiency of the equation (1) and its analogs is the fact that no recognition of age-class, nor any other vital statistic which may be pertinent including time-lagged behavior, are made (Larkin, 1963).

The paper's objectives were based on the observation that the demographic processes of tropical marine fish stocks are inter-related and evolve continuously with respect to time. These processes are believed to be influenced strongly by density-dependent population factors. Interactions with other age-strata or species means that

natural populations are usually governed by higher-order systems of equations (May, 1987). To understand the evolution of tropical multicohort fishery systems interest was directed towards developing a dynamic systems model that incorporated salient population features through attention to continuous, deterministic, nonlinear age-structured models. Thus, the paper models multiple-cohort interactions and examines the processes which may result in the predominance of certain species within a multispecies complex. Elucidation of the properties of mathematical models for single, multicohort populations is a first basic step towards understanding what is going on. The principal value of nonlinear models is that they allow consideration for the effects of crowding, resource limitation, and interaction. Inclusion of nonlinearities in the equations of age-dependent population models increases their mathematical difficulty, but also increases their reliability for physical description and behavior prediction (Webb, 1985). The mathematical underpinnings of the subject discussed are still rather esoteric by current standards in population dynamics, the central notions are elementary. The approach taken is based on the belief that more useful results are obtained from models that include essential, biologically realistic nonlinearities, than are obtained from linear models with arbitrary, auxiliary constraints.

The mathematical details of such a model are developed below.

The Multiple Cohort Model

Consider a continuous model of a long-lived organism and its population dynamics given the underlying desire to understand the individual ensemble mean characteristics of weight as well as the total population density of each age strata as a function of time. In continuously-breeding populations the intrinsic population dynamics processes consists of j cohort life stages which show dependence upon the periodicity of their entrance into the population. Each cohort life stage is affected by certain mechanisms: (1) resource assimilation rate, (2) size or age specific metabolic requirements, (3) environmental

carrying capacities for each age group, (4) competition between cohorts, and (5) population density within and among cohorts, which will cause the composite population to either increase or decrease.

Assume that mean individual weight, W_i , of the i th individual in the j th "age" (=size) class is governed by the balance between the competition for available environmental resources and the age-specific basal metabolic rate. Kitchell et al. (1977) in a bioenergetics study on perciform fishes suggested that food is consumed at a rate that is a function of the weight of an individual and the ambient temperature. The general governing equation from the classic energy balance can be written:

$$\dot{W}_i = (r_i - \alpha_i)W_i \quad (2)$$

where a dot denotes differentiation with respect to time, and

$r_i \equiv$ resource assimilation or growth rate.

$\alpha_i \equiv$ intrinsic basal metabolic costs rate.

The term r_i represents the intrinsic rate of increase which would be approached if no limitations were placed on the increase in weight of the respective cohorts if they were living alone. If we now consider that the age-specific weight of the i th individual can be influenced by its local cohort density of others of its own life stage, and the individual abundances of the other j cohort life stages then the balance equation (2) can be transformed to the more appropriate form:

$$\dot{W}_i = W_i r_i - a_i W_i N_i - \sum_{i \neq j} b_{ij} W_i N_j - \alpha_i W_i \quad (3)$$

If we set $K_i = r_i/a_i$, we find that after a little rearranging:

$$\dot{W}_i = r_i W_i \{ K_i - N_i - (\sum b_{ij}/a_i) \cdot N_j \} / K_i - \alpha_i W_i \quad (4)$$

Now define:

a_i \equiv environmental carrying capacities (i.e., intraspecific checks on the rate of increase) for the ensemble individual mean characteristics.

Σb_{ij} \equiv competition coefficient between ensemble individual i and the specific j cohort densities (i.e., provides for the effects of each cohort on its competitor). By definition $b_{ij} \geq 0 \forall ij$.

N_i \equiv population abundance for the i th individual in cohort j .

N_j \equiv population abundance for the j th cohort.

Let:
$$B_i = \sum_{i \neq j} b_{ij}/a_i \quad (5)$$

The term, B_i , represents a ratio of how much damping is generated by a competitor relative to the damping a cohort has on itself. The values of the interaction parameters, b_{ij} , represent fixed coefficients between cohorts, although changes in this parameter may be represented as a quasi-simulation of habitat modification, or population genetic changes (Larkin, 1963). Equation (4) has a competition form reminiscent of the Lotka-Volterra family of equations. The actual form, or perhaps better put, the effect of competition is now through the mean weight equation. Note, here no provision for interspecific competition has been allowed, a condition which may have importance in the analysis of tropical reef fish ecology and tropical multispecies fisheries. This feature can be accomplished by adding an averaged term, $-\Sigma \Sigma C_{ijk}(t)$, with the brackets to account for the j -cohort, k -species interactions. Further, note that a basal metabolic costs term has been added which increases the equation's ability to model known physiological mechanisms, and promotes the growing acceptance and importance of physiological processes influencing growth, survivorship, and recruitment (Hoar et al., 1979, 1983; Caddy & Sharp, 1986; P. Walsh, pers. comm.).

We now need to develop a fairly simple population balance equation; such that population growth can be represented as the outcome of the gains from births or recruitment processes, offset by losses from all sources of mortality:

$$\dot{N}_i = R_{ij} - Z_i N_i \quad (6)$$

Equation (6) varies from a standard fishery representation of the change in cohort abundance with respect to time because of the addition of the recruitment term. The recruitment term allows communication between adjacent cohort population regions as well as additions that may flow between region to region in terms of either births and/or immigration or emigration. The mortality term is also structured into an alternative form with endogenous and exogenous population forcing components, i.e:

$$\text{where} \quad Z_i = M_i(W_i^\infty - W_i) + F_i \quad (7)$$

M_i \equiv instantaneous natural mortality for ensemble individual of the j th cohort (here assumed time constant, i.e. $M \equiv M_i$).

W_i^∞ \equiv optimal weight (biomass) for the i th aged (size) individual of the j th cohort.

F_i \equiv fishing and/or predatory pressure for the i th aged (size) individual of the j th cohort. A tradeoff here may be seen whereas bigger fish at age may be less susceptible to natural mortality or predation, they are on the other hand more susceptible to fishing predation.

and

R_{ij} \equiv instantaneous rate of recruitment from the j th to the i th population cell, which in the case for recruitment to the initial age becomes,

$$R_{i=0} = \sum_{j=1}^n \left(\sum_{i=1}^m f_{ij}(W_j - W_j^\infty) \right) \quad (8)$$

with f_j \equiv fecundity of the j th age (size) class.

Fecundity per unit of parental biomass may be highly variable and dependent upon the nutritional state and size structure of the stock (Parrish et al., 1986). This implies that

the weight of a specific j th cohort may be suboptimal which would allow for dependency on age-specific reproductive input on the density-dependent factors influencing growth. If weight is suboptimal then the average cohort reproductive value will decrease, while on the other hand if weight is supraoptimal, then the reproductive value of a cohort will increase accordingly. The question of recruitment to the adult population should properly be dealt with by writing down balance equations analogous to (6) for the populations of all the various stages in the life history of the species concerned.

$$\dot{N}_i = R_{ij} - [M_i(W_i^\infty - W_i) + F_i] N_i \quad (9)$$

The natural mortality then reflects the degree of metabolic stress the population undergoes reflecting endogenous constraints and provides the couple back to the mean weight equation. The biological mechanism for the density-dependent inter-age mortality could be viewed as competition for food and space in which young cannot compete favorably with older members of the population (Botsford & Wickham, 1979). The recruitment term provides an interrelation between age (size) groups. Equation (9) as written then allows for partial selection, partial recruitment, with density-dependent features, and time dependency.

Rearranging the population derivative (9) in terms of age-specific ensemble weight:

$$W_i = W_i^\infty + \frac{1}{M_i} \left[F_i + \frac{1}{N_i} (\dot{N}_i - R_{ij}) \right] \quad (10)$$

Then taking the derivative with respect to time of the population equation now expressed in terms of average weight (10) and calling M_i (i.e. $M_i \equiv M$) a constant in time and expressing everything else a function of time leads to:

$$\dot{W}_i = \frac{1}{M} \left[\dot{F}_i + \frac{1}{N_i} \left\{ (\dot{N}_i - R_{ij}) - \frac{\dot{N}_i}{N_i} (N_i - R_{ij}) \right\} \right] \quad (11)$$

substituting (10) into equation (4):

$$\begin{aligned} \dot{W}_i = & \left\{ r_i \left(W_i^\infty + \frac{1}{M} \left[F_i + \frac{1}{N_i} (\dot{N}_i - R_{ij}) - \dot{F}_i \right] \right) \left[K_i - N_i - B_i N_j \right] \right\} / K_i \\ & - \alpha_i \left(W_i^\infty + \frac{1}{M} \left[F_i + \frac{1}{N_i} (\dot{N}_i - R_{ij}) \right] \right) \end{aligned} \quad (12)$$

and substituting for the derivative of weight (11) into (12) the full equation is:

$$\begin{aligned} & \frac{1}{M} \left[F_i + \frac{1}{N_i} \left[\left\{ (\ddot{N}_i - \dot{R}_{ij}) - \frac{\dot{N}_i}{N_i} (\dot{N}_i - R_{ij}) \right\} \right] \right] \\ = & \left\{ r_i \left(W_i^\infty + \frac{1}{M} \left[F_i + \frac{1}{N_i} (\dot{N}_i - R_{ij}) - \dot{F}_i \right] \right) \left[K_i - N_i - B_i N_j \right] \right\} / K_i \\ & - \alpha_i \left(W_i^\infty + \frac{1}{M} \left[F_i + \frac{1}{N_i} (\dot{N}_i - R_{ij}) \right] \right) \end{aligned} \quad (13)$$

and with some reorganization now let the forcing term, F , be represented as:

$$F = \frac{1}{M} \left[F_i (r_i (1 - (B_i N_j / K_i)) - \alpha_i) + (r_i R_{ij} / K_i) - \dot{F}_i \right] + W_i^\infty [r_i (1 - (B_i N_j / K_i)) - \alpha_i] \quad (14)$$

Terms will be by definition independent of N_i , but contain forcing by the deterministic parameters and the specific densities of the competing N_j cohorts. Then the j -dimensional differential equation is written as:

$$\begin{aligned} & \ddot{N}_i \left(\frac{1}{M N_i} \right) + \\ & + \dot{N}_i \left[\left(\frac{1}{M N_i} \right) \left\{ (R_{ij} / N_i) - (\dot{N}_i / N_i) + r_i (B_i N_j / K_i) - 1 \right\} + \alpha_i \right] + r_i / M K_i \\ & + N_i \left[(r_i / K_i) \left(W_i^\infty + F_i / M \right) \right] \\ & + \left(\frac{1}{M N_i} \right) \left[R_{ij} \left\{ r_i (1 - (B_i N_j / K_i)) - \alpha_i \right\} - \dot{R}_{ij} \right] = F \end{aligned} \quad (15)$$

If we substitute for the constant terms within age strata and replace B_i by (5) and K_i by r_i/a_i then:

$$A_2 = \frac{1}{M}$$

$$A_3 = r_i (1 - (B_i N_j / K_i)) - \alpha_i = r_i - \sum b_{ij} N_j - \alpha_i$$

$$A_4 = \frac{r_i}{MK_i} = \frac{a_i}{M}$$

$$A_5 = \frac{r_i}{K_i} \left[W_i^\infty + \frac{F_i}{M} \right] = a_i \left[W_i^\infty + \frac{F_i}{M} \right]$$

$$A_6 = R_{ij} (A_3) - \dot{R}_{ij}$$

$$A_7 = R_{ij}$$

Now with substitution of the intra-strata constants and some rearrangement of (15) results in:

$$\ddot{N}_i \left(\frac{A_2}{N_i} \right) + \dot{N}_i \left(\frac{A_2}{N_i} \right) \left[\frac{1}{N_i} (A_7 - \dot{N}_i) - A_3 \right] + A_4 + N_i A_5 + (A_2/N_i)(A_6) = \bar{F} \quad (16)$$

Recognizing that (16) is in the general form of the 2nd order nonlinear differential equation:

$$\ddot{N} + B_1 \dot{N}(aN + N) + B_2 N = F \quad (17)$$

Equation (17) can be recast as a second-order differential equation for a specific ensemble individual i as:

$$\ddot{N}_i = (\dot{N}_i^2/N_i) + \dot{N}_i(A_3 - (A_4/A_2)N_i) - (\dot{N}_i/N_i)A_7 - N_i^2(A_5/A_2) + N_i(F/A_2) - A_6 \quad (18)$$

Solution Schemes

As written above, the coefficients r_i , K_i, \dots , etc., are all functions of the age of an organism, and therefore if we choose the index i to follow the year class of the organism, the problem becomes a fairly complicated time integration for each year class. This can be viewed as a close parallel to the *Lagrangian* problem of following the evolution of a particle's momentum in fluid dynamics given the forcing as a function of space-time. Although the analog is not exact, like the momentum equation for fluid flows, it is a simpler task to consider the evolution at a fixed point in "age" space. In the latter case the coefficients are fixed and the problem can be solved as single levels in age given the history of the other age classes. This can be done in three models:

- (1) A locally approximate solution given the N_j 's from a "reasonable" selection of the overall solution space and then solve for a given N_i ; or...
- (2) Specify the coefficients for all age classes and then integrate the entire set using an iterative approach; or...
- (3) Linearize and abstract the system (Schaffer, 1981).

Equilibrium Analysis

The first stage in the analysis of any population model is to ask whether there is any particular size at which the population will stabilize, i.e., does the model possess any stable steady states (Nisbet & Gurney, 1982). The steady state is deterministically stable if after experiencing a perturbation the population ultimately returns to its steady state value. The ultimate behavior of many biological populations may reveal a convergence to a stable time-independent state as time evolves. The prediction and description of convergence to equilibrium states is one of the most valuable applications of mathematical population models (Webb, 1985). The multicohort population system of equations will have stationary states when all the time derivatives are set equal to zero. Under these conditions equation (13) can be rearranged to provide specific solutions of the N_j as examined in the Eulerian frame of reference, i.e. particles evolving by a fixed reference point.

Recall that the generalized parameters, K_i and B_i , can be specifically defined as $K_i = r_i/a_i$, and $B_i = \sum b_{ij}/a_i$. Utilizing this information and with some reorganization equation (13) can be rewritten as:

$$\begin{aligned}
 & \ddot{N}_i \left(\frac{1}{MN_i} \right) \\
 & + \dot{N}_i \left[\left(\frac{1}{MN_i} \right) \left\{ \frac{R_{ij}}{N_i} - \frac{\dot{N}_i}{N_i} - r_i + \sum b_{ij} N_j + \alpha_i \right\} + \frac{a_i}{M} \right] \\
 & + N_i \left[a_i \left(\frac{F_i}{M} + W_i^\infty \right) \right] \\
 & + \left(\frac{1}{MN_i} \right) \left[R_{ij} (r_i - \alpha_i - \sum b_{ij} N_j) - \dot{R}_{ij} \right] = F
 \end{aligned} \tag{19}$$

Where the forcing term is:

$$F = \frac{1}{M} [F_i (r_i - \alpha_i - \Sigma b_{ij} N_j) + a_i R_{ij} - \dot{F}_i] + W_i^\infty [r_i - \alpha_i - \Sigma b_{ij} N_j] \quad (20)$$

The forcing term F contains only terms which are independent of the specific ensemble N_i 's and thus its value is independent of the specific population cohort j . We are interested in viewing (19) from the Eulerian frame of reference by fixing a point space for the ensemble mean N_i and evaluating the specific solutions of the N_j population particles evolving past the fixed reference point. Setting $\ddot{N}_i = \dot{N}_j = 0$, equation (19) can be written as:

$$\begin{aligned} & \frac{1}{M} [F_i (r_i - \alpha_i - \Sigma b_{ij} N_j) + a_i R_{ij} - \dot{F}_i] + W_i^\infty (r_i - \alpha_i - \Sigma b_{ij} N_j) \\ & = N_i [a_i \left(\frac{F_i}{M} + W_i^\infty \right)] + \left(\frac{1}{M N_i} \right) [R_{ij} (r_i - \alpha_i - \Sigma b_{ij} N_j) - R_{ij}] \end{aligned} \quad (21)$$

With some reorganization of (21), we find that an explicit solution for a particular N_j can be achieved, viz.:

$$N_j = \frac{(N_i F_i + M W_i^\infty N_i - R_{ij})(N_i a_i - r_i + \alpha_i) + (N_i \dot{F}_i - \dot{R}_{ij})}{(R_{ij} - N_i - M N_i W_i^\infty)} \cdot \left[\frac{1}{\Sigma b_{ij}} \right] \quad (22)$$

Now let: $E_1 = N_i F_i + M W_i^\infty - R_{ij}$

Then a specific N_j reduces to:

$$N_j = - \left[\frac{(N_i a_i - r_i + \alpha_i) + N_i \dot{F}_i - \dot{R}_{ij}}{\Sigma b_{ij}} \right] \quad (23)$$

So that conveniently N_j can be expressed as a linear relation at equilibrium, i.e.:

$$N_j = A + B N_i \quad (24)$$

where:

$$A = \frac{r_i - \alpha_i + \dot{R}_{ij}}{\Sigma b_{ij}} \quad \text{and} \quad B = \frac{\dot{F}_i - a_i}{\Sigma b_{ij}}$$

Returning to the conditions of the Eulerian frame, we note that if we define $j = i+1$, then:

$$N_{j+1} = \rho N_j e^{-\epsilon t} \quad (25)$$

and the competition term for the ω th cohort becomes

$$N_\omega = \frac{1}{a_\omega} [b_{ij}(N_j) + b_{i,j+1}(\rho N_j e^{-\epsilon t}) + \dots + b_{i,\omega}(\rho N_j e^{-(\omega-1)\epsilon t})] \quad (26)$$

Solving explicitly for the specific N_j 's of the vector N_j , where the j terms range from j to ω , and $j = i+1$, we note that the vector arrangement of (24) can be represented as:

$$\begin{aligned} N_1 &= [(r_i - \alpha_i) - a_i N_i] \cdot \left[\frac{1}{b_{ij}} \right] \\ &\cdot \quad \cdot \\ &\cdot \quad \cdot \\ &\cdot \quad \cdot \\ N_\omega &= [(r_\omega - \alpha_\omega) - a_\omega N_i] \cdot \left[1 / \left(\sum_{r=0}^{\omega-1} b_{i,j+r} e^{-r\epsilon t} \right) \right] \end{aligned} \quad (27)$$

Equation (27) now represents the vector of coupled second-order nonlinear algebraic equations which represents population behavior in the multicohort density and competition dependent equations in the stationary state. We could then derive a formal result by neighborhood stability analysis in which we assume that the population is displaced slightly from its steady state value and follow its subsequent behavior, utilizing a set of relations like (27). Stationary points are found by replacing the derivatives on the left-hand side by zero and solving the K simultaneous equations. Truncating after the first derivatives gives K linear equations for the K cohorts.

$$[N'(t)] = A[N(t)] \quad (28)$$

A is a $K \times K$ matrix, and $[N(t)]$ is $K \times 1$, with densities $N_j(t)$ measured from a stationary point rather than from zero. Ecker and Gross (1986) discuss a method for solving an unlimited number of coupled nonlinear equations for physical systems. Schaffer (1981) demonstrated a method for abstracting systems of growth equations.

Scaling of Equations

Any quantity which appears in a population equation will normally have units which are products or ratios of the fundamental quantities time, distance, and population of a particular species. The fundamental quantities from which others are derived are frequently called "dimensions". A pure number or a ratio of quantities with the same dimensions is described as "dimensionless" or "normalized". Assuming the shortest time scale is the assimilation rate, $\frac{1}{r_i}$, the scaled form is:

$$\begin{aligned} N_o r_i^2 (\ddot{N}_i) + r_i N_o \dot{N}_i \left(\frac{r_i}{K_i K_o} [B_i N_j N_o - \frac{K_i K_o}{r_i} \alpha_i - \frac{K_i K_o r_i}{r_i} + N_i N_o] - \left(\frac{1}{N_i N_o} \right) r_i N_o \dot{N}_i + \right. \\ \left. + N_i N_o \left[M_i (\alpha_i W_i^\infty + r_i W_i^\infty - \frac{r_i W_i^\infty B_i N_o N_j}{K_i K_o}) - F_i F_o (\alpha_i + r_i - \frac{r_i B_i N_o N_j}{K_i K_o}) + \right. \right. \\ \left. \left. \dot{F}_i F_o r_i - \frac{r_i R_{ij} R_o}{K_i K_o} + N_o N_i \left(\frac{r_i}{K_i K_o} (F_i F_o - M_i W_i^\infty) \right) \right] + \frac{1}{N_i N_o} R_{ij} R_o = F(t) \quad (29) \end{aligned}$$

Dividing through by $N_o r_i^2$:

$$\begin{aligned} \ddot{N}_i + \dot{N}_i \left(\frac{1}{K_i K_o} [B_i N_j N_o - \frac{K_i K_o}{r_i} \alpha_i - \frac{K_i K_o r_i}{r_i} + N_i N_o] - \left(\frac{1}{N_i N_o} \right) \frac{1}{r_i} \dot{N}_i + \right. \\ \left. + N_i \left[\frac{M_i}{r_i^2} (\alpha_i W_i^\infty + r_i W_i^\infty - \frac{r_i W_i^\infty B_i N_o N_j}{K_i K_o}) - \left(\frac{1}{r_i^2} F_i F_o (\alpha_i + r_i - \frac{r_i B_i N_o N_j}{K_i K_o}) + \right. \right. \right. \\ \left. \left. \dot{F}_i F_o \frac{1}{r_i} - \frac{R_{ij} R_o}{K_i K_o r_i} + N_o N_i \left(\frac{1}{K_i K_o r_i} (F_i F_o - M_i W_i^\infty) \right) \right] + \frac{R_{ij} R_o}{N_i N_o r_i^2} = F(t) \quad (30) \end{aligned}$$

Any equations representing a real biological system should be valid irrespective of the units in which we measure the quantities involved in the system. The mathematical simplification achieved by using dimensionless variables frequently leads to some biological insight even without solving the equations. This is because dimensional analysis

can reveal groups of parameters which can be thought of as "controlling" the behavior of the system (Nisbet & Gurney, 1982).

Numerical Analysis Technique

For most continuous models analytic solutions are not possible, this is particularly true for highly complex sets of nonlinear equations. However, numerical analysis techniques are used to integrate the differential equations numerically, given specific values for the state variables at time zero (Carnahan and Wilkes, 1973). The evolutions must normally be modeled by nonlinear equations for which closed-form solutions are unobtainable. They may be readily integrated by computer algorithms, so that the response from given starting boundary conditions can be easily established. For any time step, $t \rightarrow (t + \Delta t)$, we desire to calculate the population trajectory for any cell i in region j :

$$N_i'(t+\Delta t) = N(t) + \zeta N \quad (31)$$

Once we calculate the N_i 's, we use the specific values to compute the vector of the ensemble weights, W_i , such that we can calculate specific ensemble abundances, which can then be computed directly in terms of density. The approach chosen to integrate the continuous second order nonlinear system of coupled equations was by rewriting specific dynamic difference equations for the numerical simulations. A numerical running scheme was designed to conduct the analysis and its development is outlined below:

Numerical Running Scheme

Two types of processes motivate the numerical simulation approach. One process, moving the coupled system forward in time using a single time-step approach averages the particles position ahead as a point between the present and the next time step. This system of equations can be unstable, particularly when complex second-order and higher equations are used. As a result, the forward simulations are used to generate a vector of initial state

values, given boundary conditions for the system. The vector of initial state values are then passed to the second process, a centered system of equations which averages the particles position over three time steps; centered systems are intrinsically more stable in the evolution of time.

The Forward in Time System

Given boundary conditions for a series of state values, the initial population state vector utilizing the state equations are generated in numerical simulation by the following system of forward difference equations:

Let the *second-order forward difference* be generally represented by:

$$\ddot{N}(t) = \frac{\dot{N}(t + \Delta t) - \dot{N}(t)}{\Delta t} \quad (32)$$

and the *first-order forward difference*:

$$\dot{N}(t) = \frac{N(t + \Delta t) - N(t)}{\Delta t} \quad (33)$$

Then substituting the properly time-stepped equations (33) into (32) leads to the dynamic forward second difference equation:

$$\ddot{N}(t) = \frac{N(t + 2\Delta t) - 2N(t + \Delta t) + N(t)}{\Delta t^2} \quad (34)$$

$$N(t + 2\Delta t) = \ddot{N}(t)\Delta t^2 + 2N(t + \Delta t) - N(t) \quad (35)$$

The form of the general second-order nonlinear differential equation can be rearranged to the second-order forward difference:

$$N(t) = \mathbf{F} - B_1 \dot{N}(t)(a + N(t)) - B_2 N(t) \quad (36)$$

Substituting equation (36) into equation (35) gives:

$$N(t + 2\Delta t) = \Delta t^2 \mathbf{F} - \Delta t^2 B_1 \dot{N}(t)(a + N(t)) - \Delta t^2 B_2 N(t) + 2N(t + \Delta t) - N(t) \quad (37)$$

Now substituting for the first-order forward difference term on the right-hand side of equation (37), results in the dynamic forward difference solution for simulation of the general form of the second-order nonlinear differential equations:

$$\begin{aligned} N(t + 2\Delta t) = & \Delta t^2 F - \Delta t B_1 [N(t + \Delta t) - N(t)](a + N(t)) \\ & - \Delta t^2 B_2 N(t) + 2N(t + \Delta t) - N(t) \end{aligned} \quad (38)$$

Equation (38) and its variants can generate the initial population state vector utilizing the state equations, but due to the inherently unstable properties of (38) in time evolution we now need to develop the centered relationships.

The Centered in Time System

Given the initial population state vector utilizing the state equations cast as a forward difference we now desire to compute the population state vector centered with respect to evolution in time, which are generally calculated as follows. Let the *second-order centered difference* be generally represented as:

$$\ddot{N}(t) = \frac{\dot{N}(t+\Delta t) - \dot{N}(t - \Delta t)}{2\Delta t} \quad (39)$$

and the first-order centered difference:

$$\dot{N}(t) = \frac{N(t + \Delta t) - N(t - \Delta t)}{2\Delta t} \quad (40)$$

Substituting the appropriate representation of equation (40) into (39) leads to the general form of the dynamic centered second-order difference equation:

$$\ddot{N}(t) = \frac{N(t - 2\Delta t) - 2N(t) + N(t + 2\Delta t)}{4\Delta t^2} \quad (41)$$

and

$$N(t + 2\Delta t) = \ddot{N}(t)4\Delta t^2 + 2N(t) - N(t - 2\Delta t) \quad (42)$$

If we now proceed similarly to the fashion we did in the previous section by substituting equation (36) into equation (42) we get:

$$N(t + 2\Delta t) = 4\Delta t^2 F - 4\Delta t^2 B_1 \dot{N}(t)(a + N(t)) - 4\Delta t^2 B_2 N(t) + 2N(t) - N(t - 2\Delta t) \quad (43)$$

With substitution of (40) into the right-hand side of (43) we obtain the dynamic centered difference solution for simulation of the general form of second-order nonlinear differential equations:

$$\begin{aligned} N(t + 2\Delta t) = & 4\Delta t^2 F - 2\Delta t B_1 [N(t + \Delta t) - N(t - \Delta t)](a + N(t)) \\ & - 4\Delta t^2 B_2 N(t) - 2N(t) - N(t - 2\Delta t) \end{aligned} \quad (44)$$

Equation (44) allows centered time evolution of the second-order state equations. To compute each specific $N(t + 1)$ you require $N(t)$, $N(t - 1)$, $N(t - 2)$, and $N(t - 3)$, *vis a vis*, four previous population cohort time-step values.

The Multicohort Numerical Simulation System of Equations

As evidenced by the development of the forward and centered systems of equations in the two previous sections we are now in a position to specifically write down the non-general coupled system of second-order nonlinear population density/abundance equations for multicohort-multispecies systems with age structure.

Recasting (17) as a second-order dynamical differential equation we have:

$$\ddot{N}(t) = N(t)\left(\frac{F}{A_2}\right) - \frac{\dot{N}(t)}{N(t)}(A_7) + \frac{\dot{N}(t)^2}{N(t)} + \dot{N}(t)(A_3 - \left(\frac{A_4}{A_2}\right)N(t)) - N(t)^2\left(\frac{A_5}{A_2}\right) - A_6 \quad (45)$$

Building upon the arguments presented above, (45) can be written as a forward difference

equation:

$$\begin{aligned}
 N(t + 2\Delta t) = & \Delta t^2 N(t) \left(\frac{F}{A_2} \right) - \Delta t^2 \dot{N}(t) \left(\frac{A_7}{N(t)} \right) + \Delta t^2 \dot{N}(t)^2 \left(\frac{1}{N(t)} \right) + \Delta t^2 \dot{N}(t) \left(A_3 - \left(\frac{A_4}{A_2} \right) N(t) \right) \\
 & - \Delta t^2 N(t)^2 \left(\frac{A_5}{A_2} \right) - \Delta t^2 A_6 + 2N(t + \Delta t) - N(t)
 \end{aligned} \tag{46}$$

Thus, with the appropriate substitutions of equation (33) into the right-hand side of equation (46), the *forward in time* evolution simulations for each specific cohort can be calculated by:

$$\begin{aligned}
 N(t + 2\Delta t) = & \Delta t^2 N(t) \left(\frac{F}{A_2} \right) - \Delta t (N(t + \Delta t) - N(t)) \left(\frac{A_7}{N(t)} \right) + (N(t + \Delta t) - N(t))^2 \left(\frac{1}{N(t)} \right) \\
 & + \Delta t (N(t + \Delta t) - N(t)) \left(A_3 - \left(\frac{A_4}{A_2} \right) N(t) \right) - N(t)^2 \left(\frac{A_5 \Delta t^2}{A_2} \right) \\
 & - \Delta t^2 A_6 + 2N(t + \Delta t) - N(t) \quad \forall j
 \end{aligned} \tag{47}$$

Clearly, the potential instabilities associated with an equation as complex as (47) which contains several squared first-order terms, in addition to its intrinsic second-order form, required development of the centered form of the set of coupled second-order nonlinear equations. Again, recalling the arguments presented above, equation (45) can now be transformed into a *second-order nonlinear centered dynamical difference* equation:

$$\begin{aligned}
 N(t + 2\Delta t) = & 4\Delta t^2 N(t) \left(\frac{F}{A_2} \right) - 4\Delta t^2 \dot{N}(t) \left(\frac{A_7}{N(t)} \right) + 4\Delta t^2 \dot{N}(t)^2 \left(\frac{1}{N(t)} \right) + 4\Delta t^2 \dot{N}(t) \left(A_3 - \left(\frac{A_4}{A_2} \right) N(t) \right) \\
 & - 4\Delta t^2 N(t)^2 \left(\frac{A_5}{A_2} \right) - 4\Delta t^2 A_6 + 2N(t) - N(t - 2\Delta t)
 \end{aligned} \tag{48}$$

With the appropriate substitutions of equation (40) into the right-hand side of equation (48) the centered equations with respect to time for the simulated time evolutions

for each specific cohort can be calculated as:

$$\begin{aligned}
 N(t + 2\Delta t) = & 4\Delta t^2 N(t) \left(\frac{F}{A_2}\right) - 2\Delta t(N(t - \Delta t) - N(t - 2\Delta t)) \left(\frac{A_7}{N(t)}\right) + (N(t + \Delta t) - N(t - \Delta t))^2 \left(\frac{1}{N(t)}\right) \\
 & + 2\Delta t(N(t + \Delta t) - N(t - \Delta t)) \left(A_3 - \left(\frac{A_4}{A_2}\right)N(t)\right) - 4\Delta t^2 N(t)^2 \left(\frac{A_5}{A_2}\right) \\
 & - 4\Delta t^2 A_6 + 2N(t) - N(t - 2\Delta t) \quad \forall j \quad (49)
 \end{aligned}$$

The reader should note that there is one centered difference equation like (49) for every j th cohort in the multicohort population ($j = 1, \dots, n$). Thus the coupled system of multicohort equations consists of a centered vector of state equations, one equation for each cohort.

Simulation of Nonlinear Second Order Differential Equations

Simulations were conducted to examine the behavior and stability using the dynamical numerical system of equations specified above. To understand the dynamic system behavior of the coupled equations specified by (15) and numerically approximated by equations for the forward (47) and the centered (49) systems of equations for the n -interacting cohorts, the system was parameterized for depiction of an engrauloid-type life history (Tables 1 and 2). Up to seven cohorts were followed in time evolution although the number could have arbitrarily been n -dimensional. Initial results demonstrated the classic limit cycles of the Lotka-Volterra equations referenced extensively in the nonlinear dynamical literature (Webb, 1985; Thompson & Stewart, 1986), particularly when an approximate form of (3) is simulated utilizing an insignificant metabolic costs term. For a given level of parameterization, the cohorts increase in relation to their intrinsic growth term. Dampening is introduced through density-dependence caused by the interactions of local cohorts and the overall population ceiling established by the carrying capacity of the cohort (Figure 2). In every case the population approaches some long term equilibrium state determined by the system of equations; but then experiences accelerating oscillations, finally settling into a stable limit cycle where the population(s) oscillate regularly between capacity

and zero states (Figure 2a). This was as characteristic of two cohorts as it was of five or more cohorts (Figure 2b).

Several interesting features were exemplified by the stable sets of second order coupled nonlinear equations. Examples here are presented in terms of plotting a few primary cohorts for the sake of brevity and clarity. First, by the appropriate control of the metabolic costs term and making no allowance in the time domain for recruit leakage from outside the cohort cell inherently induces an equivalent of the standard fishery reference "natural mortality" instantaneous rate terms. The decline of the cohorts is identical to an exponential-type loss function. The effect of intraspecific densities and the lack of outside recruitment produces the usual negative exponential effect (Figure 3a). This condition is intuitively appealing to the traditional fishery demographer because of its semblance to a frame of reference so typically presented. Secondly, when communication between the cohorts in terms of recruitment occurs, both in the $r(j)$ term, and pulsed with respect to the $R(i,j)$ term, we see a shifting of dominance between cohorts in time evolution (Figure 3b). These "moving" cohorts are now fully dynamic and continuous and can be affected by their ability to capture available environmental resources, cohort carrying capacities, competition among other cohorts, population density within and among age strata, their age-specific continuous recruitments from the local population, and the potential for recruitments from sources extrinsic to the local population as may be typical in many tropical fishery systems. The system of equations have been approached here classically as a problem in Lagrangian dynamics. Older age groups may damp recruitment because of their predatory effect on the younger age strata. Numerically strong population age strata can completely dominate or cause catastrophic collapse of other age strata for specific ranges of time evolution (Figure 3c,d). Very non-equilibrium type of population dynamics become prevalent. Strong cohort classes can completely dominate other age strata if the competition between the groups is intense enough. Strong competition between cohorts can cause the ensemble weight at age to fluctuate significantly through time (Figure 4c). Fishing reduces

competition by decreasing specific cohort abundances and it serves to stabilize the competition induced effects by increasing the ensemble weight per individual and thus increases the fecundity per age-specific unit of biomass. This finding is in contrast to Parrish et al.'s (1986) conclusions which stated that the reduction in age composition caused by heavy exploitation will greatly reduce the average fecundity per unit of biomass. Increased numbers of cohorts causes the total biomass to remain relatively stable suggesting one mechanism or purpose for continuous cohort production in tropical regions. The parochial fishery attitude that a strong year class or cohort is productive for the fishery may be marginally true from the perspective of current yield, but may be inaccurate when the effect of this strong cohort is such as to damp out the other local cohorts as it passes through the fishery which negatively impacts the reproductive ability of the population to support itself. Subsequent cohorts are damped by a big cohort. The system is a complicated one with switching between states.

Utilizing the set of coupled equations and a small enough parameter space it may be possible to develop an understanding where bifurcations and catastrophes may exist. The requirement for any fishery development or management program is to develop information as to what portion of the biomass is available for fishing and to allow the population to remain in a steady or increasing position. Although a population with the interaction terms addressed here is looked at cohort by cohort it appears a bumpy ride. However, if we look at the population biomass as an aggregate it gives the appearance of being a little bit damper than the individual cohorts (i.e. what about total biomass when you sum across the cohorts). Formally some equilibrium may exist, however if you push up and down on the system it begins to oscillate indicating an unstable equilibrium. Apparently stochastic dynamics arise from simple and rigidly deterministic density-dependent mechanisms. This suggests that apparently chaotic dynamics are ubiquitous dynamics and that they can arise more readily (with weaker nonlinearities) in systems of higher dimensionality. In a dissipative system where no interactions exist between the cohorts you obtain the stable

equilibrium as suggested by traditional models discussed in Ault and Fox (1988a,b,c). No matter what the initial distribution, without nonlinearities the population will contract to a fixed stationary distribution. No interactions however seemed like an unreasonable assumption based on the extensive literature indicating otherwise (see e.g. Fox, 1975; Botsford & Wickham, 1979; Daan, 1980; Caddy & Sharp, 1986; May, 1987). The limit cycles of this system suggest that the equilibrium of this system is unstable, and that possibly bifurcations exist. In other words the traditional assumptions regarding the equilibrium point may be unrealistic, and formal equilibrium does not exist. Causes of cyclical fluctuations are of considerable theoretical interest (Botsford & Wickham, 1979). When the species concerned is of economic importance they are of practical value as well. Knowledge of the specific mechanism causing cyclical fluctuations is necessary in formulation of effective fishery policy. The limit cycles viewed in the Poincare sections suggest that the limit cycles exist because of the interactions (Figure 5). Dynamic equilibrium then would be a limit cycle, and this limit cycle is bouncy. Botsford and Wickham (1979) suggested that fishery policies that involve removal of most individuals above a certain size can increase the propensity for unstable, cyclic behavior.

Clearly, we need some insight into what can happen in the evolution of a fishery system, and in the possible ways the system may be influenced by the initial conditions. The complicated behavior of simple deterministic models can have disturbing implications for the analysis and interpretation of biological data. Implications for ecological and fishery theory of high-order period and aperiodic orbits are most unsettling (May & Oster, 1976). Many systems have shown the general tendency to shift from many species to a few with exploitation over time (e.g. Gulf of Thailand, (Pope, 1979a); Gulf of Nicoya, Costa Rica (Madrigal, 1985)). The methodologies presented herein can be important for providing rare insights into the study of realistic population dynamics by the utilization of the new unique coupled set of nonlinear differential equations to assist determination of the effects of competition in harvested tropical multicohort - multispecies systems. The multicohort

model made some of the simplest assumptions for the complex processes that tropical multispecies populations undergo. However, in the attempt to model the system more appropriately the assumptions utilized are clearly an extension which attempted to be consistent, justifiable and follow thermodynamic laws. The model was developed in an attempt to ask the relevant questions of the parameters, and clearly this approach can not be any less robust than the state of the present traditional models when applied to the tropical domain.

Future Scope of the Multicohort - Multispecies Model and Extensions

While the analysis is not complete, the purpose of this paper has been to describe the multicohort nonlinear dynamic system modeling as a technique to study tropical marine fish stock(s) population dynamics processes. The unique feature of the equations presented in this section is that it represents the first time anyone has coupled an n-cohort, n-species relation and solved the system of equations. Beyond its intrinsic mathematical interest, it may have considerable significance for advancing the study and understanding of structured populations under exploitation. The multicohort model may be considered as depicting respectively the mode of action of density-independent and density-dependent factors. Accepting these parallels, the model may demonstrate some widely discussed properties of mechanisms of population regulation. Models as complex as that presented here are generally not used in fishery analysis due to the lack of adequate data to completely specify them. Indeed, the amount of data needed to completely specify a complex model of a specific population is seldom available for a real fishery. Clearly, the model of this section will provide more accurate views and predictions of system behavior as real data become available. The model developed in this section has been studied with parameters gleaned from the literature, and as such can only be used to specify general system conclusions. Data specific to a particular system will be necessary to provide a more cogent understanding of the underlying nature and behavior of the system.

However, the intent here was to expose aspects of population behavior that may otherwise be occluded by the simplifications inherent in many traditional fishery models, particularly the effects of competition and predation when added to the competing risks model. Recognition that density-dependent mechanisms can produce cyclic and sometimes chaotic behavior in fish populations does have important implications for the way that certain kinds of data are analyzed. Not even in the most exact of the physical sciences are the coefficients of any model ever known with absolute precision. As such, the model of this section may then suggest a new tact for strategies based on current data, or new kinds of data that may be of paramount importance to proper tropical multicohort, multispecies, multigear fishery management. Multiple equilibria and strange attractor states appear to become prevalent features of biological systems when interactions such as competition and density-dependencies are explicitly modeled (May 1981, 1987). A logical extension of the multicohort model would be to work out a principal components analysis that would estimate the most likely position of the system subjected to perturbation. In this case it would be possible to develop exact probabilities of system outcomes by performing a sensitivity analysis to parameter scalings and controlled perturbations in the deterministic model. Ultimately these findings could be extended these to a Markov model for the multicohort - multispecies system. It is concluded that this present formulation of intraspecific competition, together with an expanded version which may also incorporate interspecific competition, should be applied to a laboratory and/or a natural situation to test it's usefulness for prediction.

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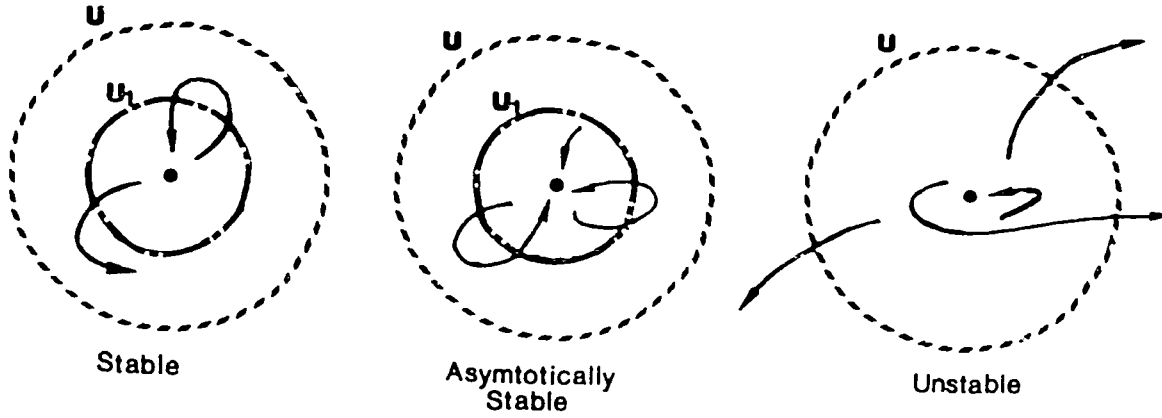
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List of Figures

- Figure 1:** Depiction of stability and bifurcations of equilibria and cycles for n -dimensional system of differential equations. Panel (A) shows three phase portraits illustrating the character of Liapunov stability for an equilibrium state (following Thompson & Stewart, 1986): (i) *stable equilibrium* point where every nearby solution stays nearby for all future time, (ii) *asymptotically stable equilibrium* because all solutions tend to equilibrium as $t \rightarrow \infty$, and (iii) *unstable equilibrium* because perturbation may lead to multiple equilibria or chaos. Panel (B) characterizes the states of equilibria portrayed in Panel (A) as a basketball on a mountainside. As the parameter space increases the system has an increasing propensity for becoming unstable.
- Figure 2:** Time evolution of the nonlinear multicohort population equations showing limit cycles for: (A) two cohorts, and (B) five cohorts.
- Figure 3:** Time evolution of the nonlinear population equations showing: (A) a large metabolic term and no recruitment communication between age strata, and (B,C,D) temporal communication between cohorts.
- Figure 4:** Simulated population cohort abundance modeled by equations (48) and (50) for the cases where: (A) the optimal weights at age strata are identical, (B) optimal weights increase with increasing age, and (C) the time evolution of ensemble weight under (B).
- Figure 5:** Domains of attraction for the phase-space trajectories showing a spectrum of limit cycles for various initial conditions and continuous recruitment: (A) system approaching a dynamic limit cycle, (B) increasing optimal weights at age increasing age strata, (C) conditions in (B) with low fishing mortality, (D-E) conditions in (B) with moderate growth term, and (F) large growth term.

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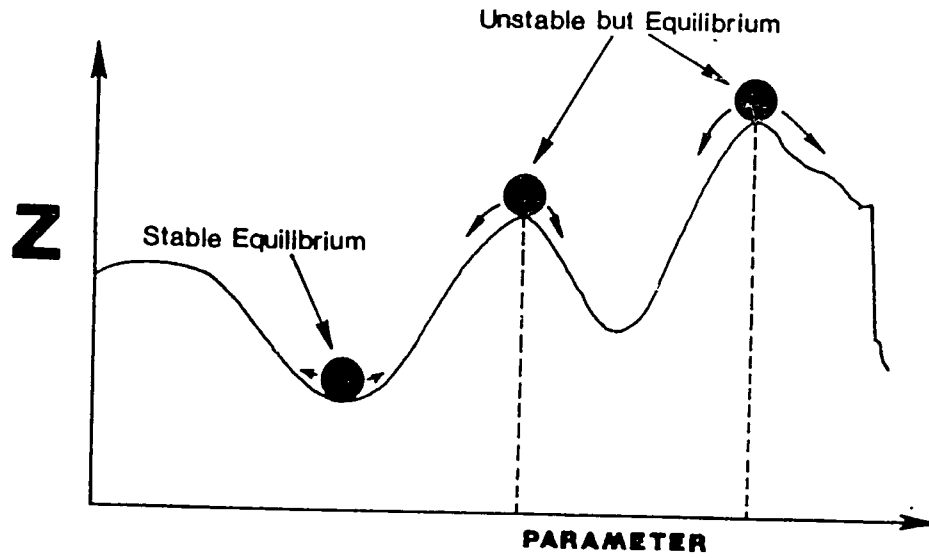
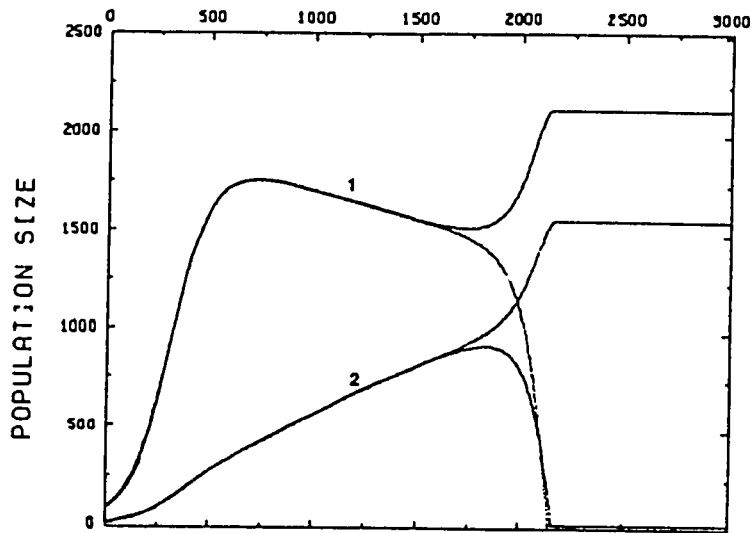


Figure 1

(A) Multicohort Population Equations
TIME EVOLUTION



(B) Multicohort Population Equations
TIME EVOLUTION

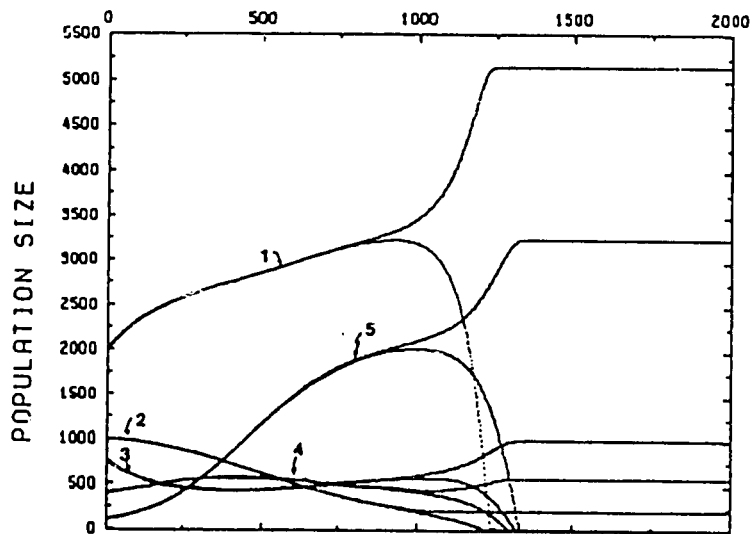
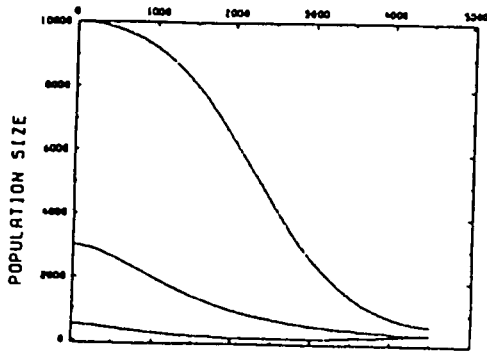
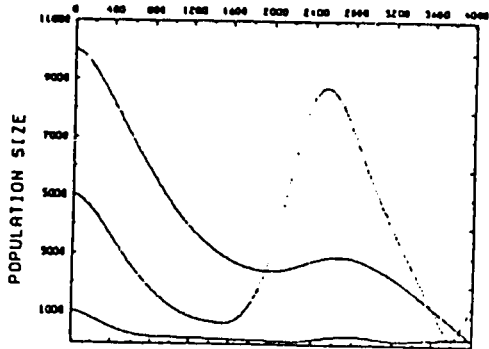


Figure 2

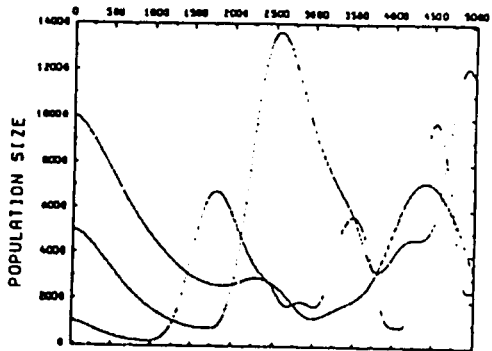
A. Multicohort Population Equations
TIME EVOLUTION



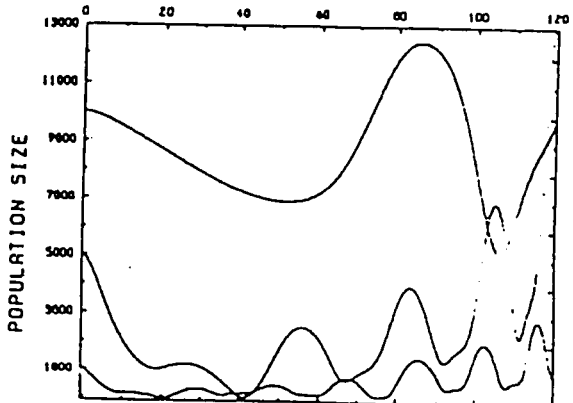
B. Multicohort Population Equations
TIME EVOLUTION



C. Multicohort Population Equations
TIME EVOLUTION



D. Multicohort Population Equations
TIME EVOLUTION ($\times 100$)



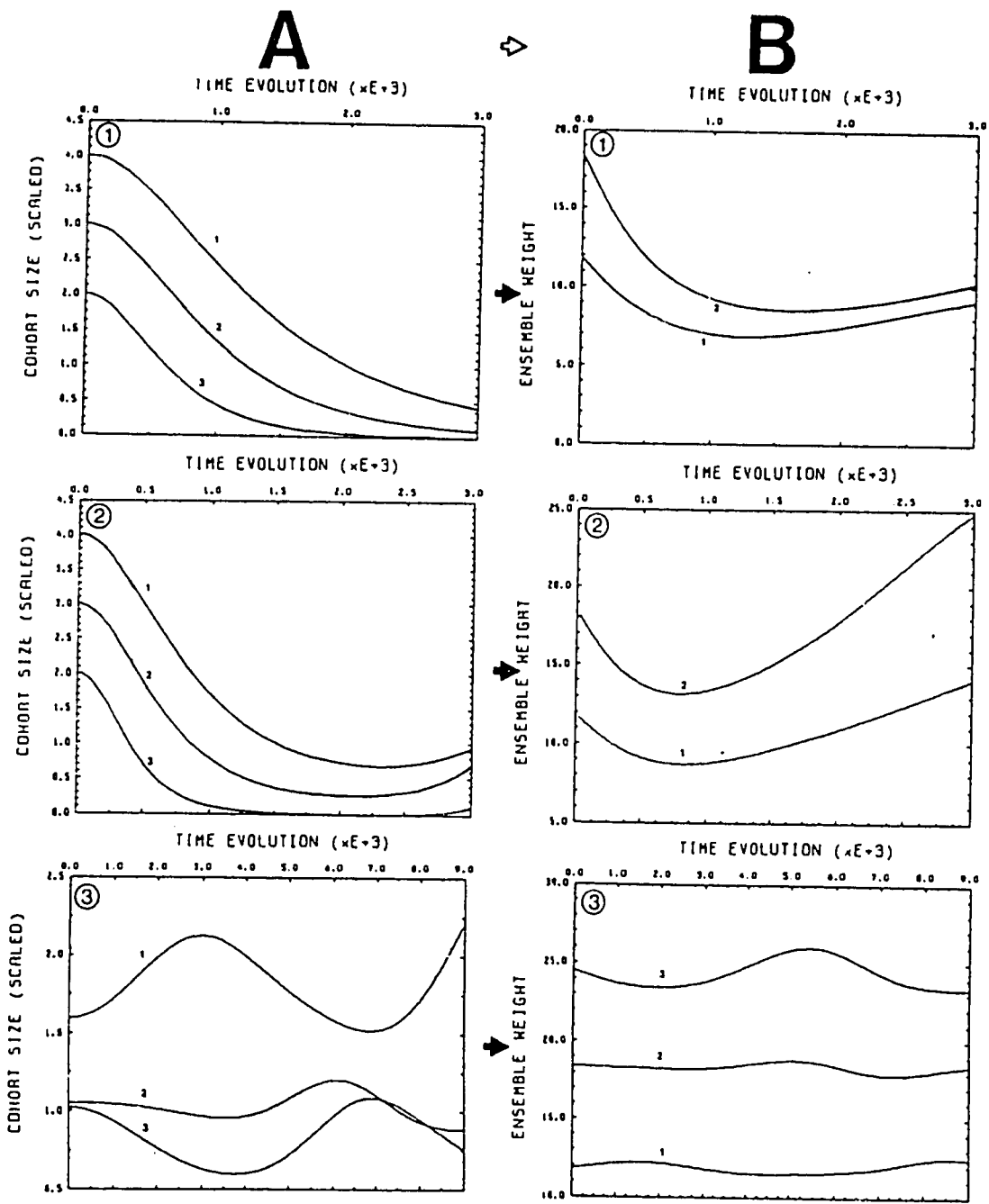


Figure 4

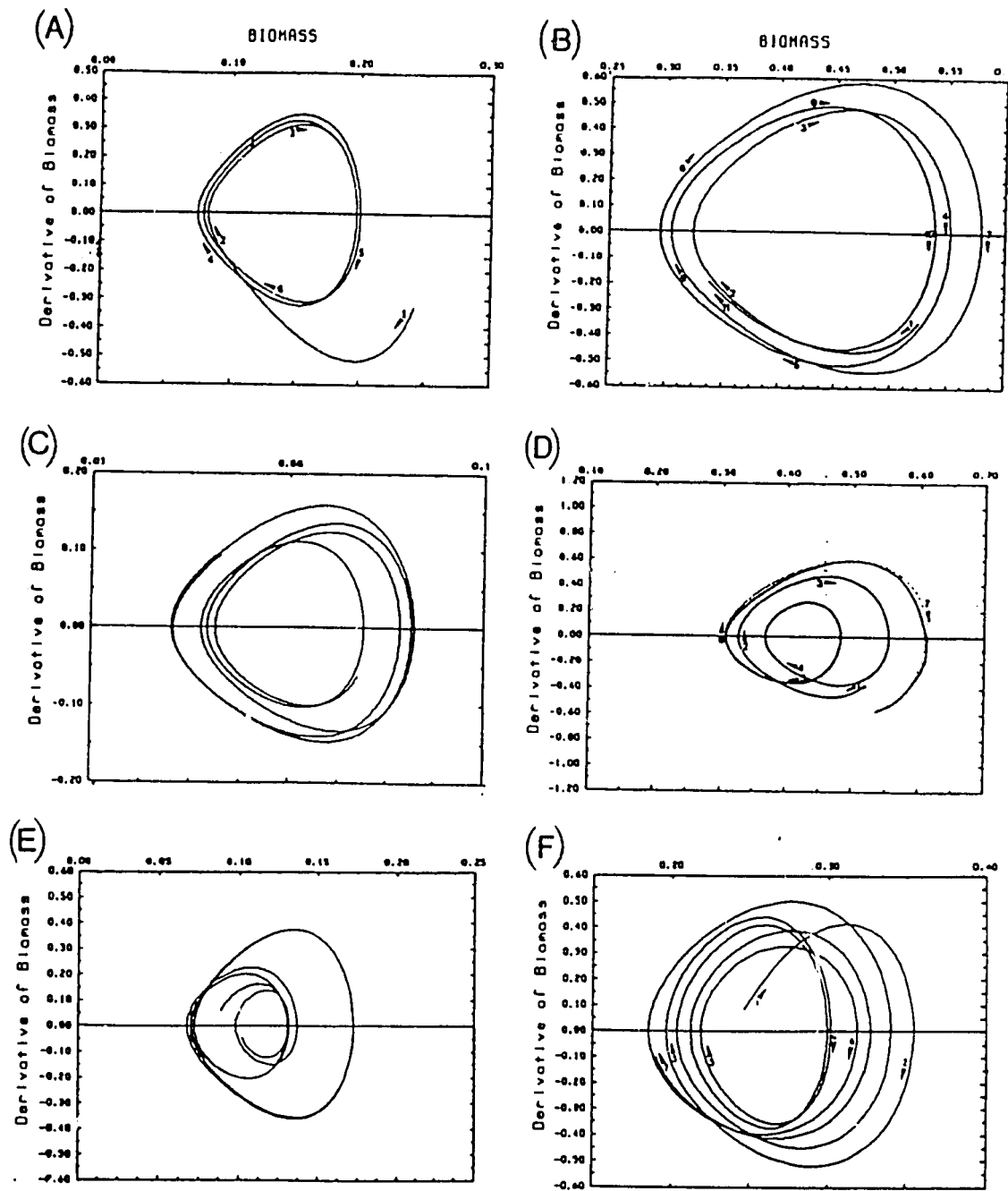


Figure 5

Table 1: Engrauloid annual rate parameters used in the continuous simulations of the second order nonlinear multicohort population model. Data from Tillman & Stadelman (1976), Hunter & Goldberg (1980), Hunter & Leong (1981), Parrish et al. (1986), Caddy & Sharp (1986).

<i>Cohort</i>	$r(i)$	$a(i)$	$m(i)$	$W^*(i)$	$f(j)$	$a(i)$
I	1.023	.0003500	1.1	11.81	1.00	0.077
II	1.012	.0007500	1.1	18.41	1.93	0.088
III	1.001	.0003913	1.1	24.50	2.93	0.099
IV	0.990	.0004444	1.1	29.68	3.88	0.110
V	0.985	.0004667	1.1	33.86	4.72	0.116
VI	0.979	.0005455	1.1	37.14	5.42	0.121
VII	0.974	.0006250	1.1	39.46	5.98	0.127

Table 2: Matrix of interaction $b(i,j)$ coefficients. Rows are the cohorts affected while the columns are the cohorts who are causing the interaction.

AFFECTS							
	1	2	3	4	5	6	7
1	XXX	.00025	.000005	.000001	.000001	.0000001	1.0E-8
2	.000125	XXX	.000125	.000125	.000125	1.0E-6	1.0E-7
3	.000225	.00035	XXX	.000125	.000025	1.0E-5	1.0E-6
4	.000	.00001	.001	XXX	.0001	.00005	1.0E-7
5	.000	.001	.001	.001	XXX	.00001	1.0E-5
6	.000	.000001	.00001	.0001	.0005	XXX	1.0E-4
7	.000	.000001	.00001	.0001	.0002	.00001	XXX